

Growth, Development, and Sexual Dimorphism in Vervet Monkeys (*Cercopithecus aethiops*) at Four Sites in Kenya

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ABSTRACT Body weight and ten body segment measurements were collected from 367 wild-trapped vervet monkeys (*Cercopithecus aethiops*) in central and southern Kenya. The animals represent between 70 and 95% of the animals in each of 30 troops at four geographical locations separated by 80 to 380 km. The capture sites differed in altitude, mean annual rainfall and temperature. Two questions are addressed: (1) what are the differences in male and female growth patterns, and (2) what is the relationship between size, climate, and availability of food? Each animal was assigned to an age class based on dental examination. Means for all variables do not diverge for males and females from birth to age class 4 (15–18 months). After this, male and female growth rates diverge. This sexual dimorphism in growth pattern may reflect timing of entry into the reproductive community. A nested analysis of variance (ANOVA) was employed to compare sites, groups within sites and individuals within groups. Statistically significant differences between sites in body weight and body segment measurements are found for adult females. Except for tail length, these differences do not follow Bergmann's or Allen's Rules correlating size differences and temperature, but rather may reflect proximity to cultivated areas or tourist lodges with greater access to human food. *Am J Phys Anthropol* 103:19–35, 1997. © 1997 Wiley-Liss, Inc.

Studies of growth and development provide information on critical developmental parameters. These parameters include the timing of sexual maturity and entry into the reproductive community as well as the degree of sexual dimorphism between males and females (Leigh, 1992). Besides providing information on development of individuals and suggesting the evolutionary forces that modify this development, growth studies can also document differences in size and shape among populations of animals living under different environmental constraints. This variation may be the result of adaptation, allowing for an examination of this evolutionary process. In this study we will examine growth and development at both

the individual level through timing of sexual maturity and sexual dimorphism and at the population level through a comparison of size and shape in four groups of vervet monkeys (*Cercopithecus aethiops*) living under different environmental conditions.

Most available ontogenetic information on nonhuman primates comes from a few samples of captive individuals maintained in laboratories or zoos where diet and environment are controlled. Relatively few spe-

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cies have been examined. Available studies on captive *Macaca mulatta* (van Wegenen and Catchpole, 1956; Wilen and Naftolin, 1976; Watts and Gavan, 1982; Schwartz et al., 1988; Wilson et al., 1989; Tanner et al., 1990), *Macaca arctoides* (Fauchaux et al., 1978), *Papio hamadryas anubis* (Glassman et al., 1984; Coelho and Rutenberg, 1989), *Pan troglodytes* (Watts and Gavan, 1982), *Pongo pygmaeus* (Fooden and Izor, 1983), *Cercocebus albigena* (Deputte, 1992), and semi-naturalistic populations of *Mandrillus sphinx* (Wickings and Dixon, 1992) and *M. mulatta* (Turnquist and Kessler, 1989) indicate that these nonhuman primates, like humans, are sexually dimorphic and bimaturic with the pattern of growth being different in males and females.

Patterns of development of sexual dimorphism appear to be species-specific (Leigh, 1992), resulting from difference in either the rate or the duration of growth in the two sexes (Shea, 1986; Gavan and Swindler, 1966; Leigh, 1992). There are few studies of sexual bimaturism in natural populations of non-human primates. These include hamadryas baboons, *Papio hamadryas* (Sigg et al., 1982), anubis baboons, *P.h. anubis* (Altmann and Alberts, 1987; Strum, 1991; Altmann et al., 1993), toque macaques, *Macaca sinica* (Cheverud et al., 1992), and vervet monkeys, *Cercopithecus aethiops sabaues* (Horrocks, 1986). All of these studies indicate that sexual dimorphism is insignificant until sometime after the third year of life.

The influence of environmental differences on the pattern and rate of development and dimorphism in any particular species is not well known. The rate of maturation for animals in the wild is not the same as the rate in captivity where food is readily available (Altmann and Alberts, 1987; Phillips-Conroy and Jolly, 1988; Eley et al., 1989). Additionally, studies on captive animals living in diverse conditions (Schwartz et al., 1988; Fauchaux et al., 1978) indicate that maturation and development are somewhat dependent on environment. However, examples of nonhuman primate species that have been sampled in more than one small part of the species range are rare. Therefore, the importance of environmental influence

upon differences in size, shape, and dimorphism is difficult to assess.

Most of the work on intraspecific differences in size due to latitude, habitat, and rainfall has been conducted on various species of *Macaca* (Albrecht, 1978, 1980, 1983, Albrecht and Miller, 1993; Fooden and Albrecht, 1993; Hamada et al., 1986), *Callithrix* (Albrecht, 1982), *Presbytis* (Albrecht and Miller, 1993), and *Papio* (Popp, 1983). These studies indicate that ecogeographic variation in primates is multifactorial with different factors influencing different primates in different situations. In some cases, body weight or mass and appendage size tend to follow Allen's and Bergmann's Rules (Hamada et al., 1986). Protruding body parts are reduced with increasing latitude, increasing altitude, or decreasing temperature while body size increases in these circumstances. However, in *M. nemestrina* (Albrecht, 1980) and *M. fascicularis* (Fooden and Albrecht, 1993) Bergmann's Rule is violated, while in *M. sinica* no ecogeographic effects are known (Albrecht et al., 1990). Popp (1983) did find a correlation between body size and rainfall among baboons. In addition, Strum (1991) reported that the presence of cultivated food resources can influence weight in baboons.

We report the results of a cross-sectional analysis of size and weight in free-ranging vervet monkeys (*Cercopithecus aethiops pygerythrus*) from Kenya. Specifically, we will examine the different patterns of growth in males and females and body size and weight differences in populations living in different ecogeographic areas.

MATERIALS AND METHODS

Ten body segment measurements and body weight were collected from 367 wild-trapped vervet monkeys (*Cercopithecus aethiops pygerythrus*) in central and southern Kenya. The animals represent 30 troops at four geographical locations separated by 80 to 380 km (for map see Dracopoli et al., 1983). These populations were sampled as part of a study of genetic variability in this species (Dracopoli et al., 1983). The capture sites differed in altitude, mean annual rainfall and temperature (Table 1). While all of the sites were woodland and riverine forest, one was surrounded by extensive cultivation. A

TABLE 1. *Trapping sites in Kenya*

		Type	Elevation (m)	Rainfall (mm)	Vegetation	Latitude/longitude
A	Samburu	Lowland	600–650	350–400	Dry grassland and thornscrub	37°30'E 2°45'S
B	Mosiro	Lowland	1,000–1,500	400–600	Heavily grazed <i>Acacia</i> woodland and savannah	36°E 1°30'S
C	Naivasha	Highland	Over 2,000	Over 600	Lakeside grassland	36°20'E 1°S
D	Kimana	Highland	750–1,000	200–400	Dry grassland and thornscrub	37°30'E 0°30'N

detailed account of the trapping procedure (Turner, 1981; Brett et al., 1982), and the distribution of the animals at the sites (Drapacoli et al., 1983) are presented elsewhere.

Between 70 and 95% of the animals in any given troop were captured and sampled. All measurements were taken by a single member of the field team to ensure consistency (Gavan, 1950). The animals were weighed on a Sohne baby scale to the nearest 0.5 g. Measurements were taken with a standard measuring tape to 5.0 mm. The following body segments were measured: tail (TL): base of tail to tip of tail (stretched), including hairs; body length (BL): external occipital protuberance to base of tail along curve of body; chest girth (CG): greatest circumference of the chest; body breadth (BB): greatest distance between tips of longest fingers when arms were spread, arm span; arm (UA): acromioclavicular joint to olecranon process of ulna when flexed; forearm (LA): olecranon process of ulna to point of flexion at carpus; hand (HD): point of flexion at carpus to tip of middle digit; thigh (UL): highest point of greater trochanter to midpoint of disto-lateral margin of lateral condyle of femur; lower leg (LL): midpoint of disto-lateral margin of lateral condyle of femur to tip of heel, foot dorsiflexed; foot (FL): distance along plantar surface heel to tip of toes.

The animal's dental complement was noted, and a cast of the upper dentition prepared using an alginate mold. The age of each animal was expressed in terms of its dental development. Ten eruption stages (classes) were defined using the dental eruption landmarks established by Ockerse (1959) from more than 3,000 captive *C. aethiops* (Table 2). Animals with all teeth erupted are considered fully adult, even though growth may continue after complete eruption of the permanent dentition. Table 2

TABLE 2. *Age classes based on dental eruption sequence with corresponding chronological ages¹*

Age class	Teeth erupting	Age (months)
0	None	<6 (days)
1	d	6–75 (days)
2	M ₁ ¹	8–12
3	I ₁	12–15
4	I ₁ ¹	15–18
5	I ₂ ² M ₂ ² P ₄ ¹	20–24
6	P ₃ ³	30–36
7	C ₁ ³	36–40
8	M ₃ ³	42–48
9	All teeth fully erupted	>48

¹ Based on Ockerse (1959).

also indicates the mean chronological age at which each dental landmark was attained in Ockerse's captive series. Eruption in the wild is likely to have been somewhat delayed, especially in the case of the later-erupting teeth (Phillips-Conroy and Jolly, 1988). For this analysis, however, relative age is more relevant than absolute age. The timing of dental development is likely to be correlated, in individuals, with that of general growth and skeletal development. Thus, using each animal's dental (rather than absolute) age as the independent variable against which body weight is plotted should presumably counteract to some extent the distortion of the "average" weight-gain curve that is incurred by pooling data from early- and late-maturing individuals in a cross-sectional sample (Tanner, 1962, 1988).

Pregnancy was determined by palpation and cystyl aminopeptidase phenotype (Drapacoli and Brett, 1982). If a fetus could be palpated we subtracted 200 g from the mother's body weight. This amount is somewhat less than the weight of a newborn vervet monkey. Females were scored as nulliparous, primiparous, or multiparous by nipple elongation (Lewis et al., 1981).

Nested analysis of variance (ANOVA) was employed to compare sites, groups within

TABLE 3. Sample size and mean \pm standard deviation for each variable by site, sex, and age class¹

	Samburu				Moiro				Natvasha				Kimana			
	Females		Males		Females		Males		Females		Males		Females		Males	
	n	\bar{x}	n	S.D.	n	\bar{x}	n	S.D.	n	\bar{x}	n	S.D.	n	\bar{x}	n	S.D.
Age class 0																
Body weight																
Body length																
Body breadth																
Chest girth																
Hand length																
Upper arm																
Lower arm																
Upper leg																
Lower leg																
Foot length																
Tail length																
Age class 1																
Body weight	3	0.87 \pm 0.07	11		1	1.09	3	1.14 \pm 0.13	2	1.10 \pm 0.27	14	0.69 \pm 0.34	1	0.91	2	0.97 \pm 0.17
Body length	3	22.50 \pm 1.00	11		1	23.00	3	26.33 \pm 1.89	2	30.25 \pm 10.25	14	19.00 \pm 5.88	1	26.00	2	26.00 \pm 1.41
Body breadth	3	40.33 \pm 1.61	11		1	43.00	3	43.00 \pm 2.65	2	45.50 \pm 7.78	7	41.00 \pm 5.69	1	43.00	2	41.00
Chest girth	2	20.50 \pm 0.71	9		1	21.00	3	20.83 \pm 0.76	2	19.75 \pm 0.35	8	18.75 \pm 3.02	1	18.00	2	18.50 \pm 0.71
Hand length	3	6.17 \pm 0.29	11		1	6.00	3	7.17 \pm 0.29	2	6.25 \pm 1.06	13	5.73 \pm 1.01	1	6.00	2	6.00 \pm 0.71
Upper arm	3	8.33 \pm 1.04	11		1	8.50	3	9.33 \pm 0.29	2	9.25 \pm 1.06	14	7.11 \pm 1.64	1	8.00	2	7.50
Lower arm	3	8.67 \pm 0.29	11		1	8.50	3	9.00 \pm 0.50	2	8.75 \pm 1.06	14	7.50 \pm 1.43	1	8.00	2	7.75 \pm 0.35
Upper leg	3	9.50 \pm 1.32	11		1	10.50	3	10.17 \pm 0.29	2	10.00 \pm 0.71	14	8.21 \pm 1.59	1	9.00	2	8.50 \pm 0.71
Lower leg	3	9.93 \pm 1.21	11		1	10.00	3	10.17 \pm 0.29	2	11.00	14	8.54 \pm 1.85	1	9.50	2	9.25 \pm 0.35
Foot length	3	8.93 \pm 0.81	11		1	10.00	3	10.17 \pm 0.29	2	9.75 \pm 1.06	13	8.27 \pm 1.48	1	9.00	2	9.25 \pm 0.35
Tail length	3	40.83 \pm 2.57	11		1	37.00	3	42.67 \pm 3.51	2	37.00 \pm 5.66	14	31.86 \pm 4.05	1	38.00	2	38.50 \pm 2.12
Age class 2																
Body weight	4	1.20 \pm 0.10	12		1	1.34	9	1.46 \pm 0.23	5	1.46 \pm 0.39	12	1.40 \pm 0.33	3	1.58 \pm 0.26	9	1.33 \pm 0.16
Body length	4	26.13 \pm 1.75	12		1	27.38	9	29.39 \pm 2.67	5	29.30 \pm 2.33	12	27.67 \pm 2.42	3	29.83 \pm 1.26	9	28.94 \pm 1.59
Body breadth	4	46.13 \pm 1.44	12		1	47.21	8	46.63 \pm 3.16	5	46.60 \pm 5.90	12	47.17 \pm 5.01	3	49.67 \pm 1.15	9	47.89 \pm 2.37
Chest girth	2	22.00	10		1	21.75	8	22.22 \pm 1.20	5	22.22 \pm 1.20	12	22.79 \pm 2.57	3	22.67 \pm 2.08	9	20.56 \pm 1.42
Hand length	4	6.88 \pm 0.85	12		1	6.83	9	7.39 \pm 0.44	5	7.10 \pm 0.74	12	7.08 \pm 0.70	3	6.83 \pm 0.29	9	6.78 \pm 0.44
Upper arm	4	9.38 \pm 0.85	12		1	9.75	9	10.11 \pm 0.78	5	9.40 \pm 1.02	12	9.46 \pm 1.18	3	9.33 \pm 0.29	9	8.89 \pm 0.49
Lower arm	4	10.13 \pm 0.25	12		1	10.00	9	10.50 \pm 0.87	5	10.00 \pm 0.79	12	9.63 \pm 1.15	3	9.67 \pm 0.29	9	9.28 \pm 0.57
Upper leg	4	10.75 \pm 0.29	12		1	11.00	9	11.17 \pm 0.90	5	11.00 \pm 1.06	12	10.96 \pm 1.72	3	10.33 \pm 0.29	9	10.11 \pm 0.42
Lower leg	4	11.63 \pm 0.48	12		1	11.08	9	11.44 \pm 1.07	5	11.20 \pm 1.15	12	11.29 \pm 2.12	3	11.17 \pm 0.58	9	10.67 \pm 0.79
Foot length	4	10.25 \pm 0.96	12		1	11.00	9	11.22 \pm 0.75	5	10.70 \pm 0.97	12	10.42 \pm 1.04	3	10.33 \pm 0.58	9	10.00 \pm 0.50
Tail length	4	43.63 \pm 3.12	12		1	40.00	9	45.89 \pm 3.69	5	39.80 \pm 3.96	12	39.79 \pm 4.69	3	44.00 \pm 5.00	9	40.00 \pm 3.25
Age class 4																
Body weight	2	1.62 \pm 0.08	5		1	1.63	4	1.61 \pm 0.11	4	1.72 \pm 0.10	4	1.60 \pm 0.28	4	1.74 \pm 0.37	4	1.78 \pm 0.18
Body length	2	29.75 \pm 1.47	3		1	30.17	4	29.88 \pm 2.14	4	32.13 \pm 1.44	4	28.75 \pm 2.84	3	29.50 \pm 1.80	4	32.75 \pm 2.50
Body breadth	2	51.50 \pm 0.71	5		1	52.20	4	47.67 \pm 4.93	4	50.75 \pm 5.25	4	49.50 \pm 1.00	3	53.67 \pm 4.04	4	53.50 \pm 3.00
Chest girth	2	24.00	4		1	22.75	4	22.75 \pm 0.96	3	23.33 \pm 0.58	4	23.75 \pm 0.50	4	24.33 \pm 2.52	4	23.75 \pm 1.26
Hand length	2	8.00	5		1	7.60	4	7.60 \pm 0.55	3	7.67 \pm 0.29	4	7.63 \pm 0.25	4	7.83 \pm 1.04	4	7.25 \pm 0.29
Upper arm	2	10.25 \pm 0.35	5		1	10.20	4	10.20 \pm 0.76	3	10.17 \pm 0.58	4	10.00 \pm 0.41	4	10.25 \pm 0.65	3	10.00 \pm 0.58
Lower arm	2	11.25 \pm 0.35	5		1	10.90	4	10.90 \pm 0.55	3	10.67 \pm 1.15	4	10.25 \pm 0.65	3	10.83 \pm 0.76	4	10.75 \pm 1.04
Upper leg	2	11.75 \pm 0.35	5		1	11.90	4	11.90 \pm 0.74	3	11.67 \pm 1.15	4	11.25 \pm 0.65	3	11.33 \pm 1.53	4	11.25 \pm 0.65
Lower leg	2	12.25 \pm 0.35	5		1	12.20	4	12.20 \pm 0.84	3	12.50 \pm 1.00	4	12.13 \pm 0.63	4	12.17 \pm 1.61	4	12.13 \pm 0.63
Foot length	2	11.75 \pm 0.35	5		1	11.50	4	11.50 \pm 0.35	3	11.17 \pm 0.29	4	10.63 \pm 0.85	4	11.13 \pm 1.04	4	11.00 \pm 0.41
Tail length	2	52.50 \pm 0.71	5		1	49.70	4	49.70 \pm 4.49	3	45.33 \pm 3.06	4	43.00 \pm 2.16	4	46.33 \pm 7.57	4	45.75 \pm 1.89

sites, and individuals within groups. F-statistics (Type III hypothesis) were computed using the general linear models (GLM) procedure of Statistical Analysis Software (SAS Institute, Inc., Cary, NC). Differences between means were assessed for significance by the t-test, with Bonferroni's correction for multiple tests.

RESULTS

The means and standard deviations for weight and measurements for each sex and age class at each site are given in Table 3. The means are diagrammatically represented in Figures 1–6.

Growth rate

Adult body weights and linear measurements are larger in males than females. In order to ascertain when this divergence occurs, we examined male and female weights and measurements over all the age classes. Male and female age class means for all variables do not diverge from birth to age class 4 (15–18 months). From age class 4 to age class 5 (20–24 months), females seem to level off for body weight and all segment measurements, followed by substantive growth until age class 7 (36–40 months). There is relatively little growth from age class 7 through age class 9 (>48 months). From age class 8 (42–48 months) to age class 9, females do not increase in size for all variables at all sites. The increase occurs only for some variables at Naivasha and Kimana, but not at the other two sites.

Males and females diverge in their growth curves between age class 4 and 5 primarily because females appear to level off for most variables until age class 7. Males exhibit substantive growth from age class 5 through 7 and they continue to grow through age class 9, which is defined by full adult dentition. In contrast to females, male growth from age class 7 through 9 characterizes most variables at all sites. By age class 7 females have reached most of their adult size, while males have not.

Size dimorphism in adults can be accounted for by males exhibiting a relatively faster growth rate from age class 5 to 9. However, because age class 9 is identified by the presence of complete adult dentition,

individuals of a chronological age range broader than that of other age classes are included in this class. The results do not reveal how much longer individuals may be growing after all teeth have erupted. Thus, there may be a greater discrepancy in size between males entering age class 9 and full adult size than for females. However, we have no way to determine this precisely.

Intersite differences

Adult size dimorphism is generally greater at Samburu and Mosiro than at Naivasha and Kimana. More intersite differences are found in adult (age class 9) females than in males (Table 4). In females, significant differences between sites occur in body weight, body length, body breadth, chest girth, hand, upper arm, lower arm, upper leg, lower leg, and foot lengths. In adult males, significant differences between sites occur in relatively few variables, body length and breadth, and tail length.

For several variables, differences are significant both among sites and among groups (Table 5). The proportion of variation attributable to either source is estimated by dividing the sum of squares of the variable by the total sum of squares. For body weight, the highest variation is among sites, followed by variation among individuals within groups. For body breadth, upper arm, upper leg, and lower leg lengths, the greater variation occurs among individuals within groups followed by intergroup variation. For chest girth, variation is among individuals, followed by differences among sites.

Pairwise comparisons (Bonferroni/Dunn t-test) for all sites are presented in Table 6. No significant differences ($P < .05$) are found between Samburu and Mosiro for any variable. Many more intersite differences occur among females than among males. Female intersite differences do not appear until age class 7, while male intersite differences are found in the very young (age class 1 and 2) and in the adult. The highest number of significant differences separate females of Samburu from females of Naivasha. Chest girth is the only variable separating females from Naivasha from females at all other sites.

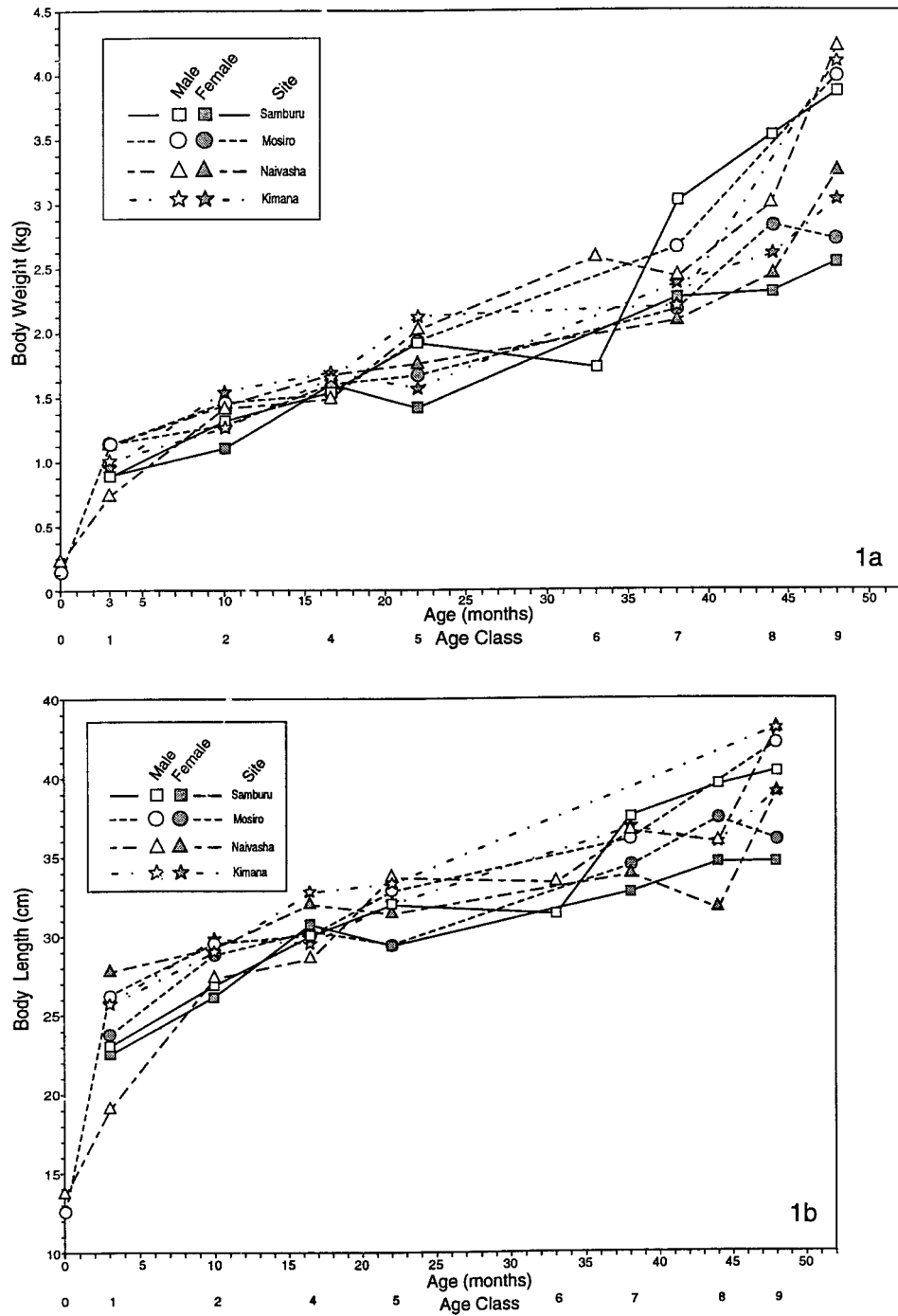


Fig. 1. **a:** Mean body weight by age class separated by sex and site. **b:** Mean body length by age class separated by sex and site.

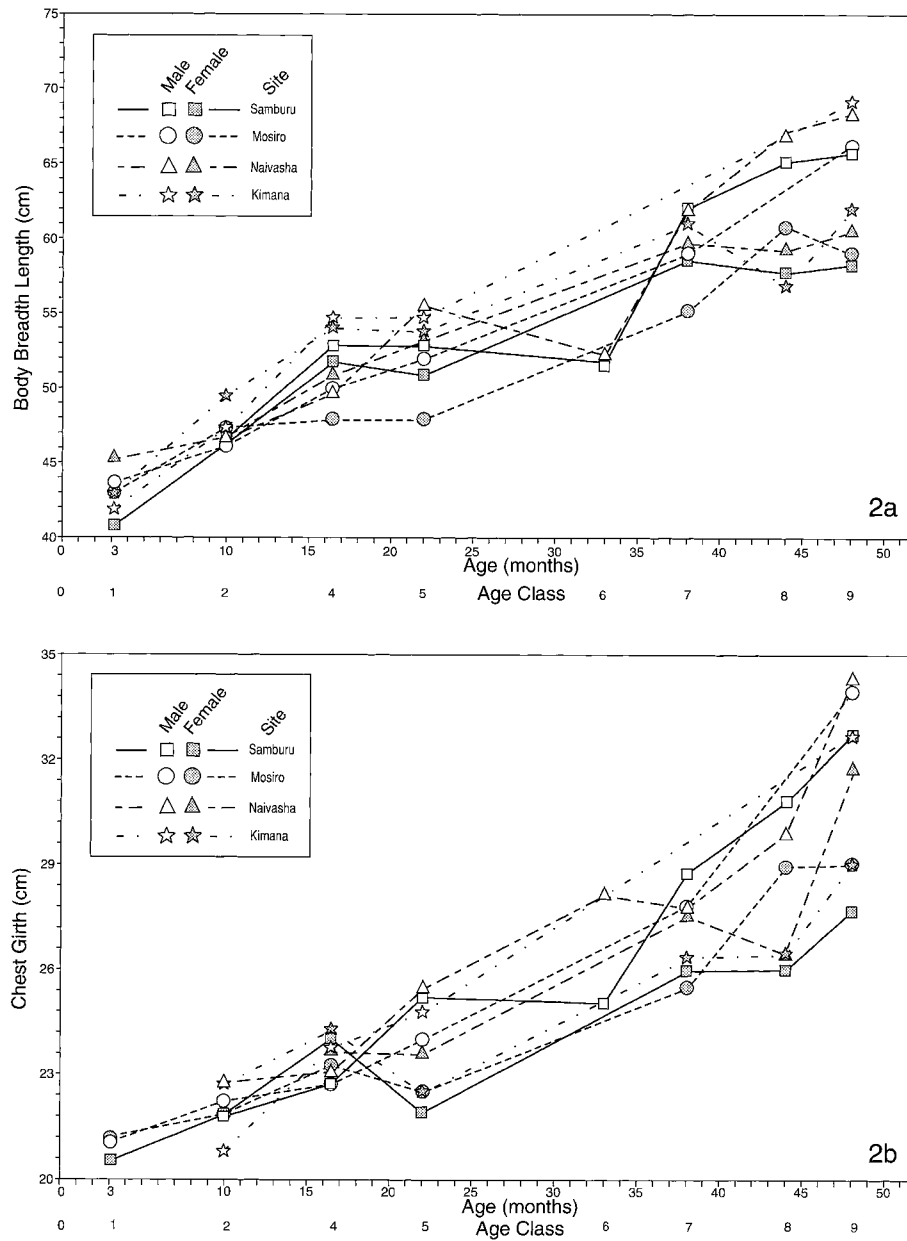


Fig. 2. **a:** Mean body breadth length by age class separated by sex and site. **b:** Mean chest girth by age class separated by sex and site.

DISCUSSION

Growth rate differences between males and females

Differences in male and female growth patterns (age of divergence of growth rates

and velocity of growth after this divergence) can be understood in terms of the earlier entry of females into the reproductive community. Males usually emigrate twice: as subadults from their natal group, and again as adults (Cheney and Seyfarth, 1983). They

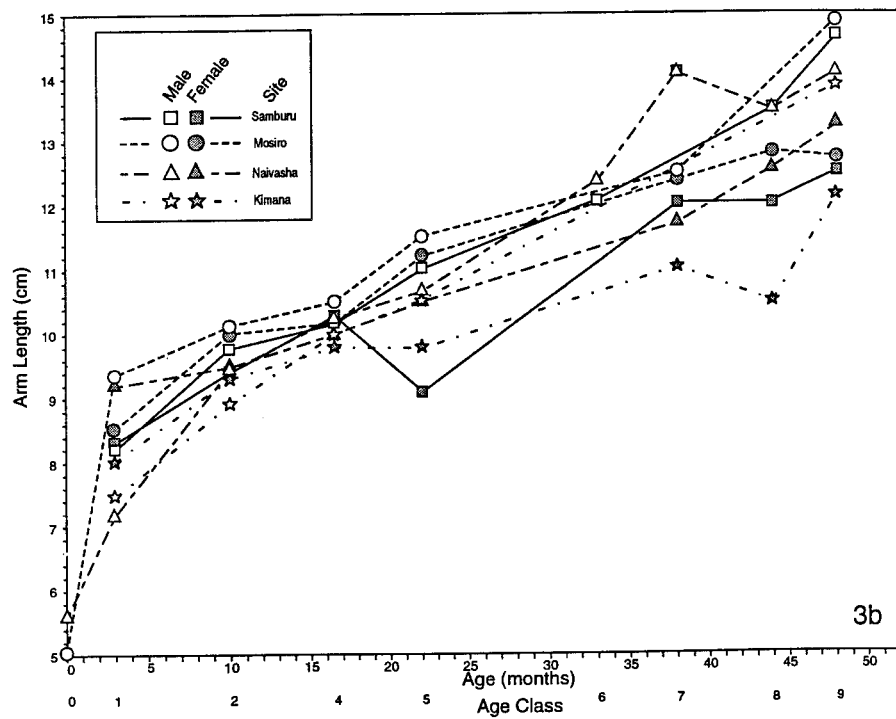
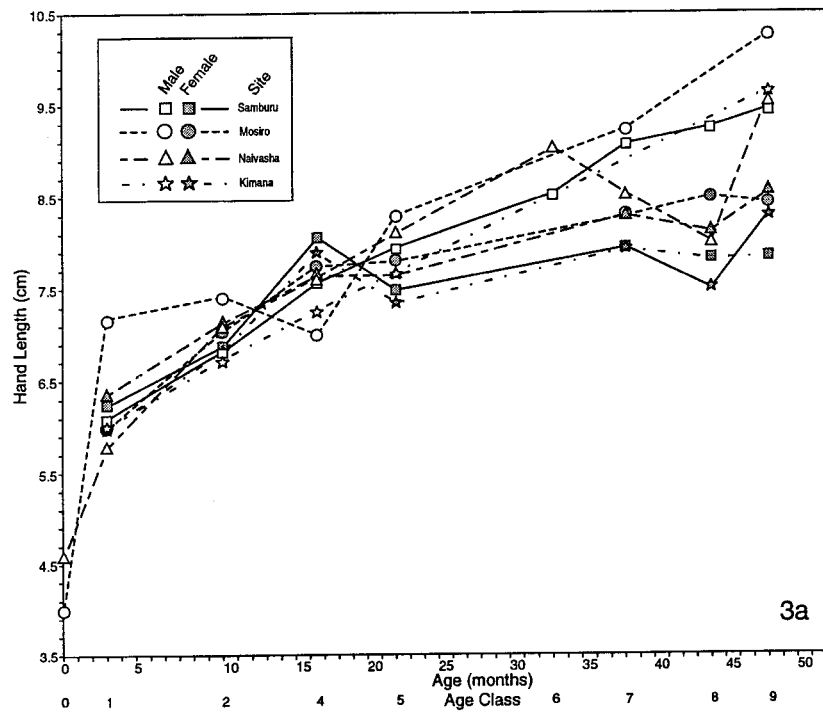


Fig. 3. **a:** Mean hand length by age class separated by sex and site. **b:** Mean arm length by age class separated by sex and site.

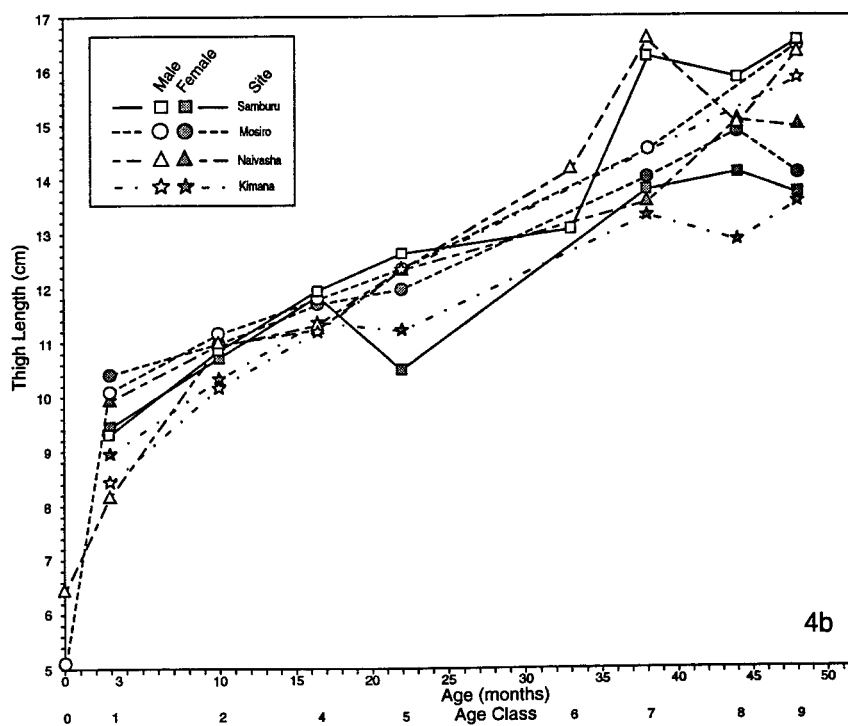
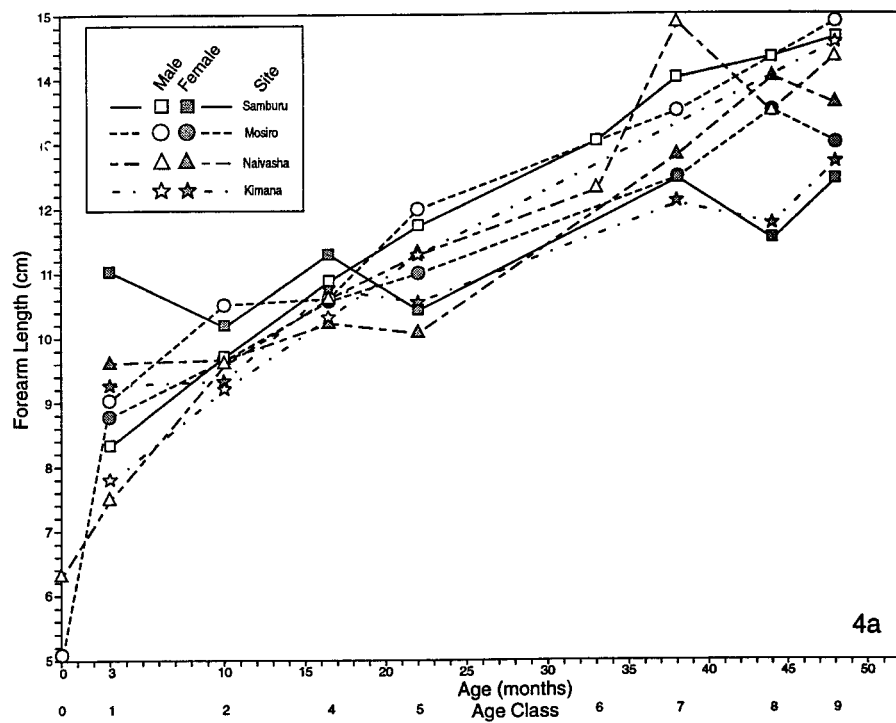


Fig. 4. **a:** Mean forearm length by age class separated by sex and site. **b:** Mean thigh length by age class separated by sex and site.

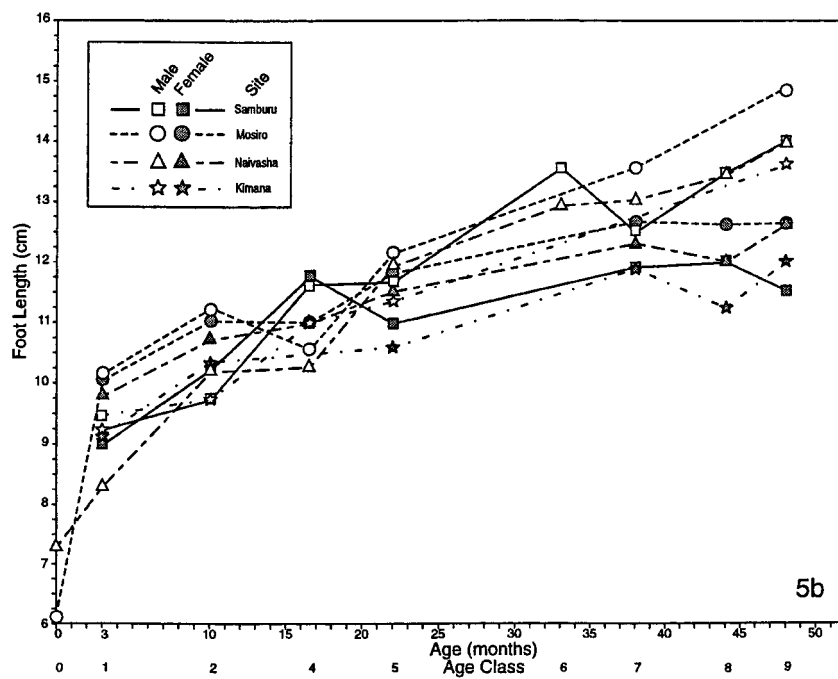
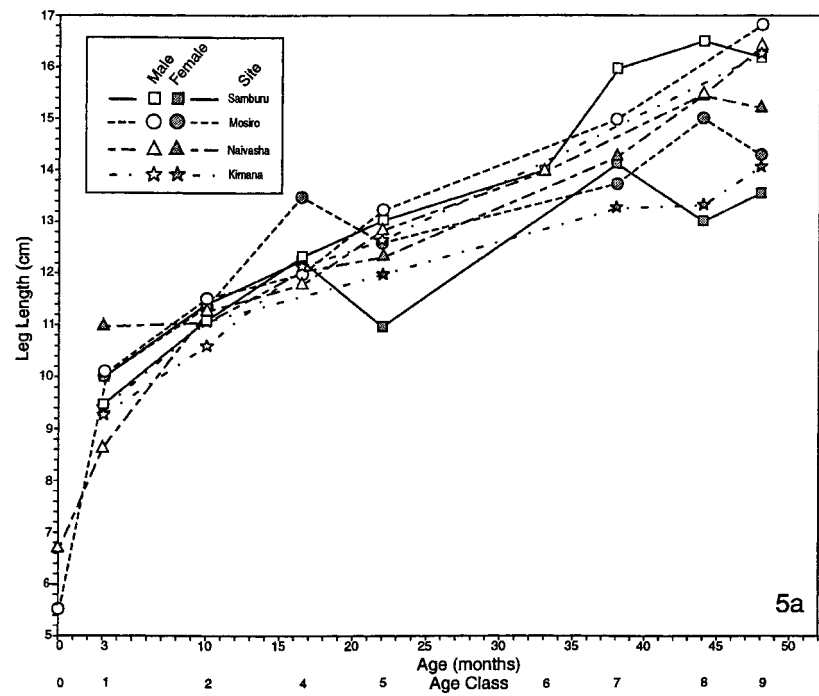


Fig. 5. **a:** Mean leg length by age class separated by sex and site. **b:** Mean foot length by age class separated by sex and site.

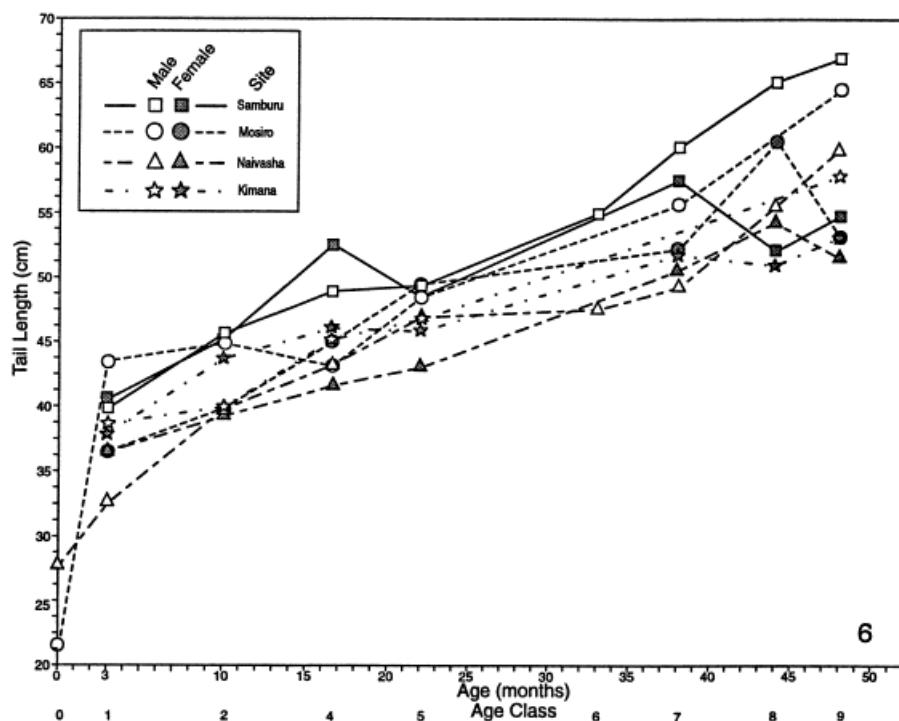


Fig. 6. Mean tail length by age class separated by sex and site.

migrate to groups where their brothers have migrated before them and join with their brothers in coalitions to successfully mate. While the exact timing of their entry into the reproductive community cannot be ascertained with the certainty of females, behavioral studies seem to indicate that this entry takes place well after acquisition of the animal's full dentition (Cheney and Seyfarth, 1983).

Females enter the reproductive community as subadults, somewhere between 30 and 36 months of age. Primiparous females have a dental age of approximately 40 months. Since gestation is approximately 22 weeks (Rowell and Richards, 1979), females enter the reproductive community at approximately 36 months. This timing is suggested by behavioral observations (Cheney and Seyfarth, 1983), by nipple elongation (Lewis et al., 1981), and by the presence of STLV-I and SIVagm antibodies (Dracopoli et al., 1986; Phillips-Conroy et al., 1994).

It appears that females attain skeletal maturity at about the time they begin repro-

ducing. The same is true of males; however, males enter the reproductive community later than females.

Growth rate differences between sites

Statistically significant differences in body weight and body segment measurements between sites are found in age class 9 females. Of the four sites in this sample, two, Samburu and Kimana, are lowland and two, Mosiro and Naivasha are highland. The four sites differ in mean annual temperature and rainfall as well as altitude. The highland sites have a lower mean annual temperature and greater annual rainfall than the lowland sites. Naivasha, the highest and wettest site, is also the most intensely cultivated. Large farms, as well as small plots of cultivated land are found throughout the area. The vervets in this area are notorious crop raiders. Kimana has some cultivated land, but it is much less cultivated than Naivasha.

Body measurements of a single species living under these diverse conditions pro-

TABLE 4. Ratio of male to female variable means separated by site and age class

	Age class						
	1	2	4	5	7	8	9
Samburu							
Body weight	1.00	1.13	1.01	1.33	1.36	1.57	1.61
Body length	1.02	1.05	1.01	1.08	1.15	1.14	1.16
Body breadth	.98	1.02	1.01	1.06	1.07	1.12	1.16
Chest girth	.95	.99	.95	1.13	1.11	1.18	1.18
Hand length	.98	.99	.95	1.06	1.14	1.19	1.21
Upper arm	.98	1.04	1.00	1.22	1.17	1.13	1.18
Lower arm	.96	.96	.97	1.11	1.13	1.24	1.18
Upper leg	.98	1.01	1.01	1.20	1.18	1.13	1.20
Lower leg	.94	.95	1.00	1.18	1.13	1.27	1.20
Foot length	1.05	.98	.98	1.05	1.05	1.13	1.20
Tail length	.98	1.02	.95	1.02	1.06	1.23	1.21
Mosiro							
Body weight	1.05	1.09	.99	1.13	1.23		1.54
Body length	1.10	1.01	.99	1.11	1.06		1.17
Body breadth	1.10	.99	1.04	1.12	1.08		1.15
Chest girth	.99	1.01	.98	1.06	1.10		1.17
Hand length	1.20	1.06	.91	1.06	1.11		1.21
Upper arm	1.10	1.01	1.03	1.01	1.02		1.20
Lower arm	1.00	1.05	1.01	1.08	1.09		1.15
Upper leg	.97	1.02	1.01	1.03	1.04		1.17
Lower leg	1.02	.99	.96	1.05	1.09		1.19
Foot length	1.02	1.02	.95	1.03	1.08		1.18
Tail length	1.15	1.15	.94	.99	1.03		1.20
Naivasha							
Body weight	.63	.96	.93	1.15	1.00	1.29	1.29
Body length	.63	.94	.89	1.04	1.08	1.14	1.10
Body breadth	.90	1.01	.98	1.06	1.04	1.12	1.14
Chest girth	.95		.97	1.07	1.02	1.13	1.09
Hand length	.92	1.00	1.00	1.05	1.04	1.00	1.11
Upper arm	.77	1.01	1.03	1.01	1.20	1.04	1.06
Lower arm	.86	.96	1.01	1.10	1.19	.96	1.06
Upper leg	.82	1.00	1.01	1.00	1.22	1.00	1.10
Lower leg	.78	1.01	.98	1.04	1.27	1.00	1.09
Foot length	.85	.97	.93	1.04	1.06	1.13	1.12
Tail length	.86	1.00	1.00	1.08	.97	1.02	1.12
Kimana							
Body weight	1.07	.84	1.02	1.30			1.37
Body length	1.00	.97	1.11	1.02			1.10
Body breadth	.95	.96	1.00	1.05			1.12
Chest girth	1.03	.91	.98	1.09			1.12
Hand length	1.00	.99	.93	1.04			1.15
Upper arm	.94	.95	1.02	1.08			1.14
Lower arm	.97	.96	.99	1.06			1.15
Upper leg	.94	.98	.99	1.10			1.16
Lower leg	.97	.96	1.00	1.05			1.16
Foot length	1.03	.97	.98	1.07			1.14
Tail length	1.01	.91	.99	1.00			1.07

vide data that can be used to test Bergmann's and Allen's Rules. Bergmann's Rule states that "within a polytypic warm-blooded species, the body size of the sub-species usually increases with decreasing mean temperature of its habitat" (Harrison et al., 1988). Allen's Rule extends Bergmann's Rule and states that "in warm-blooded species, the relative size of exposed portions of the body decreases with the decrease of mean

temperature" (Harrison et al., 1988). In primates, the correlations with body size have been extended to ecogeographic gradients of latitude and altitude (Albrecht, 1978) and to differences in rainfall (Popp, 1983).

Two predictions can be tested about the relationship between size, climate, and availability of food. Bergmann's and Allen's Rules suggest that the animals at the highest site will be the heaviest in body weight and the largest in chest girth, while having the shortest limbs and tails. These rules also predict a continuum in these features from the lowest to the highest sites. An alternative hypothesis suggests that greater rainfall, producing a more abundant food supply, will produce animals that are heavier and larger in all body segments than animals living in drier areas.

There are significant differences in limb proportions between Samburu and Naivasha and Kimana and Naivasha (Table 6). Table 7 indicates the means for measurements for adult females at all four sites. Each measurement is divided by the cube root of mean body weight. Body weight in females is the only measure that increases with increasing altitude, decreasing temperature, and increasing rainfall. No other measure except tail length follows the pattern expected by Bergmann's and Allen's Rules. The length of the arms and legs is not consistent with a decrease of appendage size with ecogeographical variables. Additionally, no cline is observed in the size of any variable except tail length as altitude and temperature change. In males, tail length also differs significantly between sites, with males at Naivasha having the shortest tails. Allen's Rule may be operating on tail length in these populations.

The animals at Naivasha, where food is most abundant, are not larger in all body measurements. Increased rainfall and increased food are not causing an increase in all dimensions. The only dimension in Naivasha that is absolutely larger is weight in adult females. Pregnancy is ruled out since Naivasha weights were taken after the birth season. The females at this site are heavier than those at other sites; this may be due solely to the greater availability of human food at this site. Downhower (1976) and

TABLE 5. Analysis of variance table for all variables separated by sex and age class¹

	Among sites					Within groups				
	df	SS	MS	F	Pr > F*	df	SS	MS	F	Pr > F*
Males, age class 9										
Body weight						16	12.594	0.787	2.25	0.019
Body length	3	100.035	33.345	2.83	0.071	16	188.263	11.766	1.96	0.043
Body breadth	3	117.983	39.328	2.64	0.085					
Hand length						16	11.918	0.745	2.47	0.011
Upper arm						16	32.960	2.06	2.46	0.011
Lower arm						16	30.501	1.91	1.87	0.054
Upper leg						16	53.806	3.36	4.62	0.000
Lower leg						16	43.788	2.74	5.75	0.000
Foot length						16	17.202	1.08	2.52	0.009
Tail length	3	387.857	129.286	2.64	0.085					
Males, age class 5										
Body weight						8	1.164	0.145	3.07	0.044
Body length						8	65.337	8.167	4.45	0.013
Chest girth						8	25.111	3.139	2.38	0.091
Lower arm						8	7.762	0.970	3.05	0.045
Tail length						8	828.049	103.506	10.41	0.000
Males, age class 4										
Foot length	3	2.788	0.929	5.10	0.029					
Tail length	3	193.147	64.382	5.59	0.023					
Males, age class 2										
Body length	3	36.235	12.078	2.61	0.082					
Upper arm						19	24.069	1.267	2.77	0.016
Upper leg						19	40.389	2.126	3.04	0.001
Lower leg						19	54.118	2.848	2.43	0.080
Tail length	3	339.807	113.269	6.83	0.003					
Males, age class 1										
Upper arm	3	14.590	4.863	4.72	0.024					
Upper leg	3	13.387	4.462	2.69	0.098					
Foot length	3	10.164	3.388	4.70	0.024					
Tail length	3	449.748	149.916	9.75	0.002					
Females, age class 9										
Body weight	3	11.651	3.884	14.16	0.000	21	5.761	0.274	1.76	0.043
Body length	3	384.982	128.327	27.36	0.000					
Body breadth	3	259.135	86.378	4.59	0.013	21	395.551	18.835	1.78	0.041
Chest girth	3	142.311	47.437	9.04	0.001	20	104.970	5.249	1.66	0.071
Hand length	3	7.428	2.476	4.39	0.015					
Upper arm	3	14.321	4.774	2.78	0.066	21	36.008	1.715	1.79	0.038
Lower arm	3	16.718	5.573	9.99	0.001					
Upper leg	3	18.440	6.147	2.57	0.081	21	50.205	2.391	3.14	0.000
Lower leg	3	30.663	10.221	6.08	0.004	21	35.328	1.682	2.17	0.009
Foot length	3	8.902	2.967	2.89	0.059					
Tail length						21	570.500	27.167	1.55	0.089
Females, age class 7										
Body length	3	43.552	14.517	2.92	0.077					
Body breadth	3	113.471	37.824	3.21	0.062					
Chest girth	3	12.537	4.179	3.09	0.072					
Lower leg						12	16.440	1.370	4.60	0.011
Tail length	3	149.339	49.780	4.35	0.027					
Females, age class 5										
Upper arm						4	7.175	1.794	21.53	0.015
Upper leg						4	7.842	1.960	47.05	0.005
Lower leg	3	3.310	1.103	0.49	0.709	4	9.042	2.260	10.85	0.040
Females, age class 4										
Body weight						6	0.438	0.073	5.37	0.098
Body breadth						5	83.417	16.683	9.69	0.045
Chest girth						5	13.417	2.683	12.07	0.034
Upper arm						5	2.292	0.459	8.25	0.056
Tail length						5	133.167	26.633	5.45	0.097
Females, age class 2										
Body weight						6	0.733	0.122	12.06	0.033

¹ df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-statistic calculated.

* Pr > F, the probability that the table value for F is greater than the calculated value provided for cases where Pr > F is < .10.

TABLE 6. Variables for which significance is indicated between sites using Bonferroni (Dunn) *t*-test¹

	S vs. N	S vs. K	M vs. N	M vs. K	N vs. K
Males					
Age class 9	BL, HD	BL, HD, TL			
Age class 2	TL	TL	TL	LA, TL, UA	CG
Age class 1	TL		TL		
Females					
Age class 9	BW, BL, BB, CG, UA, LA, UL, LL, FL	BW, BL, BB, HD	BW, BL, CG	BL, BB	CG, UA, LA, UL, LL
Age class 8		UA	BL	UA	UA
Age class 7	TL	BL	CG	BB	

¹ Sites: S, Samburu; M, Mosiro; N, Naivasha; K, Kimana. Variables: BW, body weight; BL, body length; BB, body breadth; CG, chest girth; HD, hand length; UA, upper arm; LA, lower arm; UL, upper leg; LL, lower leg; FL, foot length; TL, tail length.

TABLE 7. Variable means (from Table 2) divided by the cube root of body weight for adult (age class 9) females¹

	Samburu (n = 39)	Mosiro (n = 10)	Naivasha (n = 32)	Kimana (n = 15)
BW ^{1/3}	1.37	1.40	1.51	1.47
BL	25.17	25.71	25.71	26.35
BB	42.15	41.67	40.12	42.45
CG	20.28	20.75	20.92	19.77
US	18.14	18.25	17.76	16.91
LA	18.14	18.25	17.76	16.91
HD	7.16	6.25	6.11	5.76
UL	9.99	10.00	9.86	9.21
LL	9.92	10.21	13.63	9.59
FL	8.60	9.00	8.32	8.16
TL	40.39	38.64	35.21	36.89

¹ See Table 6 legend for variable abbreviations.

Ralls (1977) suggest that small size in females may be advantageous in a fluctuating environment, allowing for an increased sensitivity to environmental changes indicating favorable breeding conditions. There is no indication that adult females at other sites are smaller than females at Naivasha: they are not as heavy.

Observations in primates and other mammals indicate that the addition of human food to natural foraged food may cause the animals to grow faster, to achieve their final weight at an earlier age, and to have a higher final weight (Strum, 1991). Rats, prairie dogs, deer, and squirrels reach puberty earlier if they are located in areas of extra food near cities (Sadleir, 1969). Pastured cattle fed on a diet supplemented by human food reach adult weight earlier than penned cattle without supplements (Bronson, 1989). !Kung women living at cattle-posts are heavier and taller at each stage of the developmental process than !Kung women living a traditional hunter/gatherer lifestyle (Howell, 1979).

While studies of weights in wild primate populations are rare, two studies of baboons provide the clearest analogies to the vervets in this study. Strum (1991) reports on the baboons at Gilgil in Kenya. Of the troops she observed some were crop raiders and others were not. Asymptotic body weights of the raider females were considerably higher than those of the non-raider females. These trends were not so clearly visible in males. Strum accounts for this sex difference by the fact that female raiders remain in their natal group their entire lives, while males migrate to other groups, and thus spend only part of their lives in raider groups. Altmann et al. (1993) studied baboon populations at Amboseli in Kenya. One of the troops studied obtained its food from a garbage dump. Females who had access to this abundant food had an average body mass 50% greater than wild feeding females. The differences in garbage dump males and wild feeding males was not so great. Altmann et al. (1993) also account for this sex difference by the fact that males disperse and experience differing feeding conditions during their lifetimes. The addition of human food caused this additional increase in weight.

A question that arises from the observation of weight differences between wild-feeding animals and those supplementing with human food is whether these weight differences are due to additional caloric intake or to a decrease in activity. Vervets eat flowers, seeds, leaves, and other small objects. Smith (1977) analyzing the natural diet of *Alouatta* found that only about 50% of the food could be assimilated. Human food, on the other hand, is larger, does not have protective toxins or other physical protective

features, and has a higher digestibility. However, Altmann et al. (1993) found that the caloric intake of garbage dump and wild-feeding baboons was approximately the same. The difference was in the amount of physical activity required to obtain food. When food availability was high, physical activity decreased. Garbage feeders expended 16% less energy than wild feeders in obtaining food. This accounts for the increase in weight.

The situation at Naivasha is very similar to the garbage dump feeding or crop raiding of the baboons. Human food is available without considerable energy expenditure. And, as with the baboons, females are the most responsive to this increase in food availability and decrease in caloric expenditure. The Kimana females, while not as heavy as the Naivasha females, are heavier than the females at Samburu and Mosiro. Kimana is a lowland site with some cultivation. It is not as extensively cultivated as Naivasha. Some human food is available, but not as readily available as at Naivasha. Thus, it seems likely that the addition of readily available human food is causing the increase in the single dimension of weight.

CONCLUSIONS

Cross-sectional data of 367 vervet monkeys indicate that these animals are sexually dimorphic and bimaturic. Female growth levels off at an earlier age than male growth. This leveling off corresponds to their entry into the reproductive community. After the leveling off, the velocity of growth is greater for males than for females. Males who may migrate more than once before entering the reproductive community do not attain their full size until about 2 years later than females.

Additional conclusions about the relationship of size and environment derive from a comparison of animals from four sites differing in altitude, temperature, rainfall, and availability of human food. Tail length appears to follow Allen's rule for decreasing size of appendages in colder climates. No other appendage follows this pattern. In addition, animals in areas of more rainfall seem to be heavier. However, there is no consistent pattern between altitude, rain-

fall, and overall size. Females at the highest and wettest site are the heaviest. However, this increase in weight is not accompanied by a corresponding increase in body dimensions, suggesting that it is not temperature or rainfall dependent. Rather, this site is the most cultivated and the animals are crop raiders, and as with other primates that routinely consume human food, they are heavier than their wild-feeding counterparts. Whether the significant factor at Naivasha is an increase in calories or a decrease in energy expenditure cannot be determined. We can conclude that there is considerable variance in female size and this may be driven by a variety of factors which can include among other things activity, nutrition, and feeding behaviors.

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